A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 102: 191–207 (2025)
DOI: 10.3897/neobiota.102.144004

Research Article

Epiphytic algae mitigate the inhibitory effects of two aquatic invasive plants, *Pontederia crassipes* and *Pistia stratiotes*, on a submerged plant community

Yi-Luan Shen[1,2], Jing-Fang Cai[1,2], Jing-Jing Xue[1,2], Xiao-Li Yang[1,2], Da-Zhi Wang[1,2], Hong-Li Li[1,2]

1 *School of Ecology and Nature Conservation, Beijing Forestry University, Beijing 100083, China*

2 *Key Laboratory of State Forestry and Grassland Administration on Ecological Protection in the Yellow River Basin, Beijing Forestry University, Beijing 100083, China*

Corresponding author: Hong-Li Li (lihongli327@163.com)

Abstract

Exotic plant invasions and epiphytic algae potentially influence the growth of submerged plants. However, the effect of epiphytic algae on the resistance of submerged native plants to plant invasion is elusive. Therefore, we conducted this study to explore the effects of invasion scenarios and epiphytic algae on a submerged plant community (*Hydrilla verticillata*, *Potamogeton wrightii*, and *Vallisneria natans*) and water quality. We set up a control experiment with four invasion scenarios (no invasion, *Pontederia crassipes* invasion, *Pistia stratiotes* invasion, and co-invasion of *P. crassipes* and *P. stratiotes*) and two epiphytic algal states (with and without epiphytic algae). The presence of invasive plants resulted in significantly lower biomass ($P < 0.01$) of the submerged plant community without epiphytic algae than that with epiphytic algae, and the community biomass was lowest in the case of co-invasion. The presence of epiphytic algae resulted in native plants exhibiting competitive interactions only during co-invasion, whereas native plants exhibited competitive interactions at all times in the absence of epiphytic algae. Total nitrogen and phosphorus contents in water were lowest in the absence of invasion. Additionally, total phosphorus contents was highest in the presence of epiphytic algae and co-invasion. These results demonstrate that co-invasion strongly inhibits the growth of submerged plant communities more than single invasions, and epiphytic algae potentially offset this suppression. These findings will provide a scientific basis for submerged native plant restoration in wetland ecosystem.

Key words: Co-invasion, native plants, plant invasion, plants restoration, water quality

OPEN ACCESS

Academic editor: Pedro Anastácio
Received: 10 December 2024
Accepted: 21 April 2025
Published: 7 October 2025

Citation: Shen Y-L, Cai J-F, Xue J-J, Yang X-L, Wang D-Z, Li H-L (2025) Epiphytic algae mitigate the inhibitory effects of two aquatic invasive plants, *Pontederia crassipes* and *Pistia stratiotes*, on a submerged plant community. In: Anastácio P, Ribeiro F, Chainho P (Eds) Invasions in Aquatic Systems. NeoBiota 102: 191–207. https://doi.org/10.3897/neobiota.102.144004

Copyright: © Yi-Luan Shen et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Submerged plants are primary producers, providing abundant food and habitat for aquatic biota and aiding in water purification (Jeppesen et al. 1997; Li et al. 2023; Liao et al. 2024). Therefore, submerged plants are critical in maintaining the biodiversity and stability of shallow lake ecosystems (Liu 2021). However, invasions contribute significantly to the decline and extinction of submerged plant communities (Phillips et al. 2016). Invasive plants reproduce rapidly and occupy crucial ecological niches, floating invasive plants can form a dense meadow on the water surface, competing with submerged plants for light, nutrients, and other resources (Fleming and Dibble 2014). Plant invasions are frequently accompanied by changes in the aquatic environment, further degrading the submerged plant community (Zhou et al. 2017; Yuan et al. 2023).

Plant invasions are prevalent, and ecological niches of certain invasive plants overlap such that ecosystems are co-invaded by two or more plants (Wang et al. 2020; Wei et al. 2020). The frequent interaction between invasive plants impacts native plant communities in these co-invaded ecosystems (Zhong et al. 2022; Li et al. 2024). Negative interactions between invaders can moderate their impacts on native plant communities (Wang 2016). On the other hand, invasive species can mutually contribute to their establishment, further accelerating the invasion process and causing more severe impacts on native plants, a phenomenon known as invasional meltdown (Simberloff and Von Holle 1999; Wang 2016). A study showed that the co-invasion of two invasive plants *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L. can impose synergistic impacts on soil bacterial richness, thereby facilitating their subsequent invasion (Wei et al. 2020). Not only will the co-invasion of plants cause more serious damage, but the co-invasion of plants and herbivores will also have similar effects; herbivory by the invasive snail *Pomacea canaliculata* may enhance the invasiveness of *Myriophyllum aquaticum* (Vell.) Verdc. (Yan et al. 2022). Compelling evidence indicates that single-species invasions are detrimental to native plant communities, and the invasional meltdown hypothesis continues to be validated at the same time (Kuehne et al. 2016; Yan et al. 2022). However, the interactions between co-invading plants in aquatic ecosystems and their effects under extreme invasion on native submerged plant communities remain elusive.

Numerous biological and abiotic factors regulate the effects of plant invasion on submerged plant communities, including epiphytic algae, water nutrients, temperature, and water depth (Huang et al. 2023; Peng et al. 2023; Yuan et al. 2023). Among these regulatory factors, epiphytic algae, as a biotic factor, also potentially impact the invasion resistance of submerged plant communities (Song et al. 2017; Lv et al. 2023). Epiphytic algae form a biofilm on the surface of submerged plant stems and leaves, forming complex interactions, competitive or symbiotic, with submerged plants (Cattaneo et al. 1998; Zhang et al. 2023; Alena et al. 2025). On the one hand, excessive epiphytic algae inhibit the growth of submerged plants by competing for light and nutrients, ultimately causing the collapse of submerged plants and turning the water from clear to turbid (Asaeda et al. 2004; Min et al. 2017). On the other hand, epiphytic algae can promote plant growth by aiding in nitrogen fixation (Dai et al. 2023), complicating the effects of epiphytic algae on submerged plants. However, in aquatic ecosystems where plants co-exist, the effect of epiphytic algae on the resistance of communities of submerged plants to invasion remains unknown.

As common invasive species in aquatic ecosystems, *Pontederia crassipes* and *Pistia stratiotes* L. cause evident damage and ecological pollution to submerged plant communities, and there are numerous studies on their invasion mechanisms (Zhou et al. 2017; Qian et al. 2022). However, there is relatively limited research on the effects of epiphytic algae on the resistance of submerged plant communities to the co-invasion of *P. crassipes* and *P. stratiotes*. Therefore, in this experiment, we developed a submerged plant community with four invasion scenarios (no invasion, *P. crassipes* invasion, *P. stratiotes* invasion, and co-invasion of *P. crassipes* and *P. stratiotes*) and two epiphytic algae (with and without epiphytic algae) treatments to test our proposed hypotheses: (1) Co-invasion suppresses the submerged plant community more than single invasions; (2) Epiphytic algae increase the resistance of submerged plant community to co-invasion.

Materials and methods

Experimental design

The experiment was conducted in the experimental base of Sanqing Park, Beijing Forestry University, Haidian District, Beijing, China (40°0'28.17"N, 116°20'17.64"E), from June 10 to July 28, 2023. The submerged and invasive plants used in the experiment were collected from an aquatic plant breeding base in Suqian City, Jiangsu Province, and were cultured in water for two weeks before the commencement of the experiment.

According to previous research (Fletcher et al. 2023; Ma et al. 2023), we set the experimental period as 48 days, and used 25 L plastic buckets (38 cm high, 32.5 cm diameter at the upper mouth, 27.5 cm diameter at the lower mouth) as the experimental container, with the bottom filled with 15 cm of substrate (sand, soil ratio 2: 3, soil was collected from the fields of Sanqing Park). Submerged plants with favorable and comparable growth conditions were selected and planted uniformly in the experimental buckets, each of which included four individuals of each submerged plant species (*Hydrilla verticillata* (L. f.) Royle, *Potamogeton wrightii* Morong, and *Vallisneria natans* (Lour.) H. Hara. Initial length of *H. verticillata* and *P. wrightii* was roughly 15 cm, initial length of *V. natans* was roughly 10 cm).

The experimental setup comprised groups of epiphytic algae and non-epiphytic algae. Submerged plants with the epiphytic algae group were planted directly in the experimental buckets, while submerged plants without epiphytic algae group were carefully brushed with a soft-bristled brush in clean water to remove epiphytic algae on the surface of the leaves before planting in the experimental buckets. In addition, four different invasion scenarios were established, namely, no invasion, *P. crassipes* invasion with four individuals, *P. stratiotes* invasion with four individuals, and co-invasion of *P. crassipes* and *P. stratiotes*, with two individuals of each species (Fig. 1). Invasive plants covered about 95% of each experimental bucket. There were 8 treatments, each with 5 replicates, and plants were watered at regular intervals to maintain the water depth at 20 cm.

Sampling and parameter detection

All submerged and invasive plants were harvested at the end of the experiment, and water samples were collected from each experimental bucket. The biomass of submerged and invasive plants was measured by drying them in an oven at 70 °C for

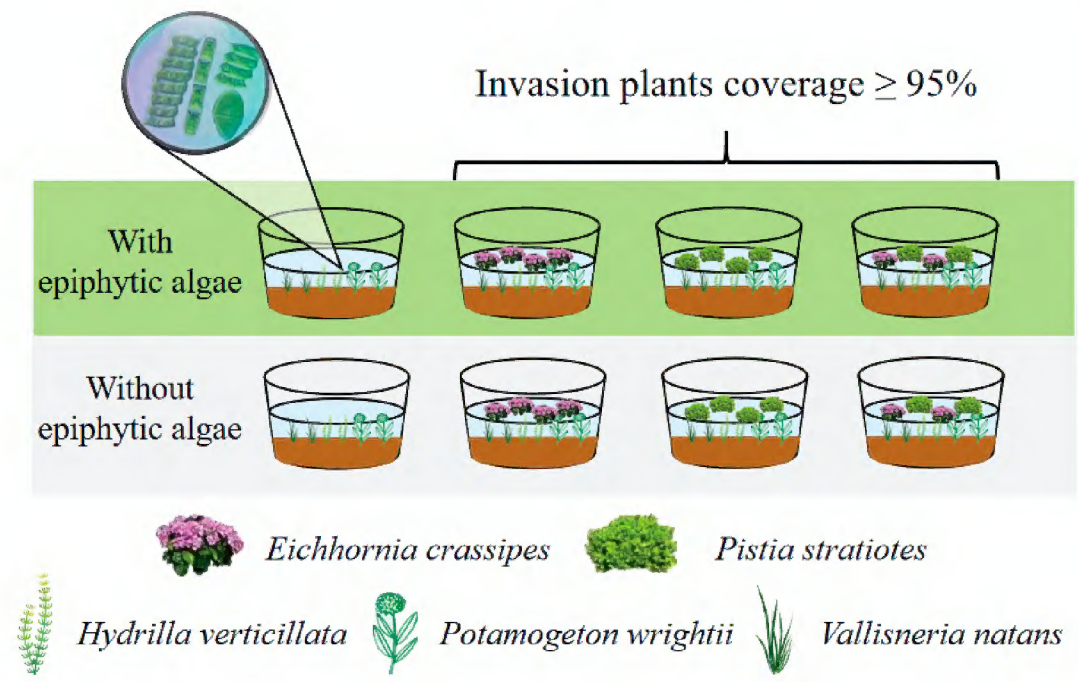

Figure 1. Experimental design.

48 hours until a constant weight was achieved. Water quality tests for collected water samples included total nitrogen content (TN), total phosphorus content (TP), transparency, pH, and dissolved oxygen (DO). The water TN content was evaluated using ultraviolet spectrophotometry with alkaline potassium persulfate digestion, whereas the water TP content was assessed by ammonium molybdate spectrophotometry. Transparency was evaluated using the Secchi disk method, and water pH was determined using a water quality detection pen (TDS-PH-EC). The DO content was measured using a portable dissolved oxygen (JPB-607A) analyzer. Of these, TN and TP measurements were done in the laboratory, and DO, pH and transparency were measured at 10:00 a.m. on the day plants were harvested. The above measurement methods all refer to our previous research methods (Shen et al. 2023).

Statistical analysis

The competition effects (CE) of invasive plants on submerged plants were determined from the biomass of each plant acquired by drying and weighing using the following formula (Wang et al. 2023):

$$CE = \ln(R_0/R_s) \quad (1)$$

Where R_0 denotes the total biomass of the submerged plant community in the absence of invasive plants, and R_s denotes the total biomass of the submerged plant community in the presence of invasive plants. A positive value for the calculated competition effect value implied that the invasive plants inhibited the growth of the submerged plant community, and the larger the value, the stronger the inhibition effect. A negative value for the competition effect implied that the invasive plants promoted the growth of the submerged plant community.

The relative dominance index (RDI) of invasive plants in treatments with the presence of invasive plants was calculated as follows (Yuan et al. 2013):

$$RDI = A/(A+B) \quad (2)$$

Where A denotes the biomass of invasive plants in the treatment in the presence of invasive plants, and B denotes the total biomass of the submerged plant community in the same treatment.

The diversity index of the community (Shannon-Wiener diversity index) was calculated according to the following formula:

$$H = -\sum P_i \ln (P_i) \text{ (i = 1, 2, 3 ..., S)} \quad (3)$$

Where S denotes the number of species in the community, and P_i denotes the biomass of species i divided by the sum of the biomass of all community species.

The evenness index (Pielou evenness index) was calculated from the diversity index using the following formula:

$$E = \mathrm{H}/\ln (S) \quad (4)$$

Where S denotes the number of species in the community, and H denotes the Shannon-Wiener diversity index.

Data analysis

A two-way ANOVA was applied to determine the effects of invasion scenarios, epiphytic algae, and the two-way interaction on community indexes (including diversity index, evenness index, total community biomass, and competition effect), the biomass and relative dominance index of invasion plants, as well as the TN, TP, transparency, pH, and DO of the water. A one-way analysis of variance (ANOVA) was employed to evaluate significant differences between treatments. Before ANOVA was performed, all data were tested for normality and homogeneity of variances.

Pearson correlation analysis was employed to evaluate associations between invasive plants, physical and chemical properties of water, and submerged plant communities. Structural equation modeling was used with the piecewiseSEM R package to assess the effects of invasive plants' and water's physical and chemical properties on submerged plant communities. Structural equation modeling involves treating each influencing factor as an independent observed variable. In this view, we first constructed a model that incorporated all possible paths and then used regressions to refine the model, yielding the final structural equation model. The standard regression coefficient, or path coefficient between indicators, was used to quantify the effects of invading plants and physical and chemical properties of water on the submerged plant community. Furthermore, the model fit was evaluated using AIC, *P*-Value, Fisher's C, and Chi-Square.

Submerged plant community metrics were calculated in Excel, while correlation analyses of invasion scenarios, epiphytic algae, and submerged plant community growth were performed in R 4.3.3. All plots were generated in SigmaPlot 14.0.

Results

Characteristics of the submerged plant community

The invasion scenarios and epiphytic algae had significant effects on the biomass of *H. verticillata* and *P. wrightii*. The interaction between the two factors had a significant effect on *H. verticillata*, while the invasion scenarios, epiphytic algae, and their interaction had no significant effect on the biomass of *V. natans* ($P < 0.05$, Table 1). The invasion scenarios had significant effects on all community indicators, including total biomass, Shannon-Wiener diversity index, Pielou evenness index, and competition effect ($P < 0.05$, Table 1). But epiphytic algae only significantly affected total biomass and competition effect. The interaction between the two factors was only significant for total biomass ($P < 0.05$, Table 1).

Table 1. ANOVA results on the effects of invasion scenarios (I) and epiphytic algae (E) on the indicators of submerged plant communities.

Indicators	Invasion scenarios (I)	Epiphytic algae (E)	I × E
Biomass of *Hydrilla verticillata*	**11.135*****	**12.377****	**4.378***
Biomass of *Potamogeton wrightii*	**3.296***	**16.839*****	2.066
Biomass of *Vallisneria natans*	0.747	2.667	2.025
Total biomass	**4.479****	**24.798*****	**5.051****
Shannon-Wiener diversity index	**14.341*****	0.952	0.154
Pielou evenness index	**16.058*****	0.087	1.172
Competition effect	**3.492***	**41.014*****	0.706

†: Significant values of F are shown in bold; *** denotes $P < 0.001$, and ** denotes $P < 0.01$.

The trend of changes in the biomass of *H. verticillata* was consistent with the changes in the total biomass of community. Only when there was no invasion, the biomass of *H. verticillata* without epiphytic algae was higher than that with epiphytic algae (Fig. 2A). Except for co-invasion, the biomass of *P. wrightii* with epiphytic algae under other conditions was higher than that without epiphytic algae (Fig. 2B). For *V. natans*, only when *P. crassipes* invaded alone, the biomass with epiphytic algae was higher than that without epiphytic algae, while under other treatment conditions,

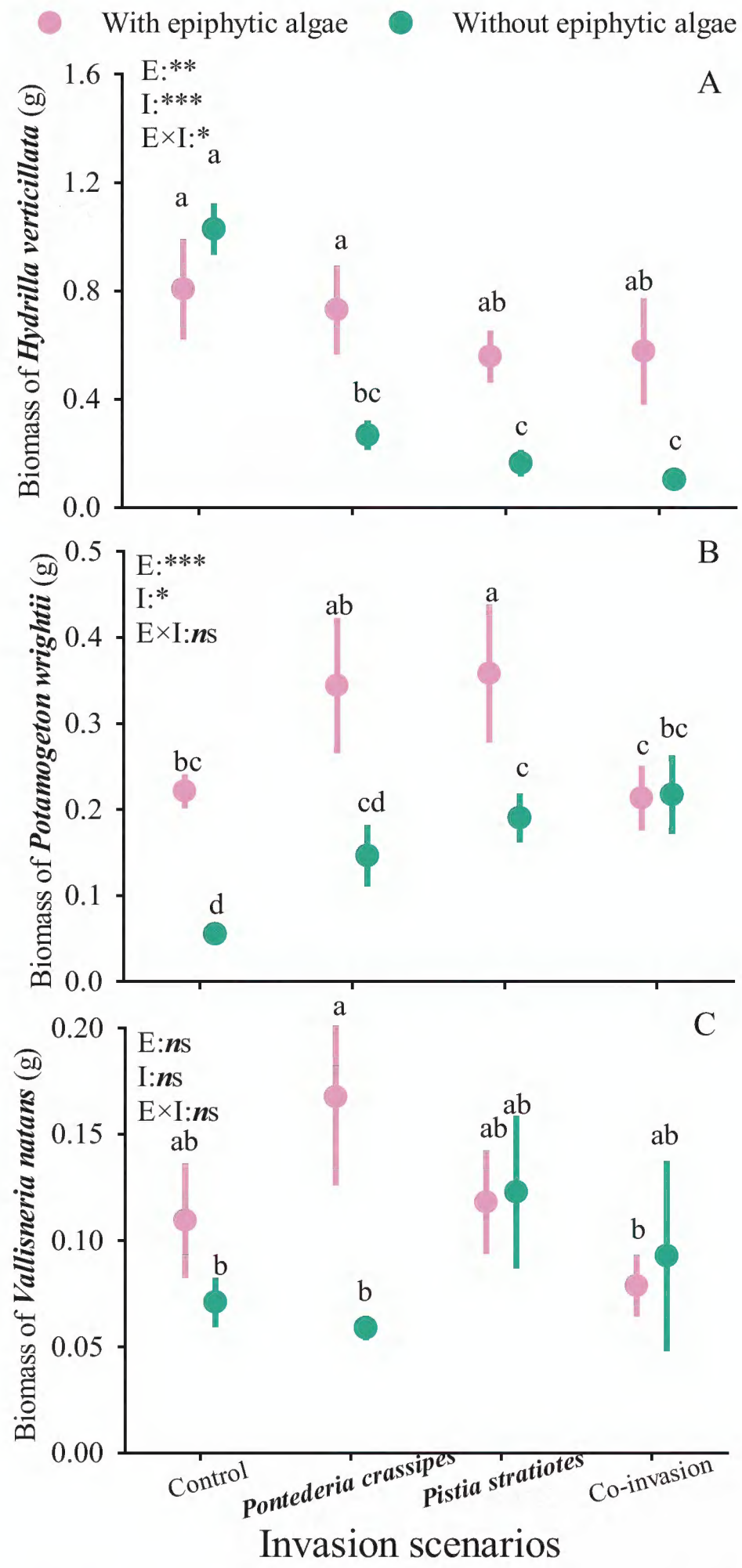

Figure 2. Effects of invasion scenarios (I) and epiphytic algae (E) on biomass of three submerged plants (mean + SE, n = 5). Control denotes "no invasion"; *Pontederia crassipes* denotes "*Pontederia crassipes* invasion"; *Pistia stratiotes* denotes "*Pistia stratiotes* invasion"; co-invasion denote "co-invasion of *Pontederia crassipes* and *Pistia stratiotes*"; * denotes "$P < 0.05$"; ** denotes "$P < 0.01$"; *** denotes "$P < 0.001$." Different letters indicate significant differences among treatments ($P < 0.05$).

there was no significant difference (Fig. 2C). Total community biomass was higher in the absence of invasion without epiphytic algae than with epiphytic algae, but the opposite effect was observed in the presence of invasive plants, with total community biomass being lowest in the co-invasion scenario (Fig. 3A). The diversity and evenness indices of plant communities were lowest in the absence of invasion (Fig. 3B, C).

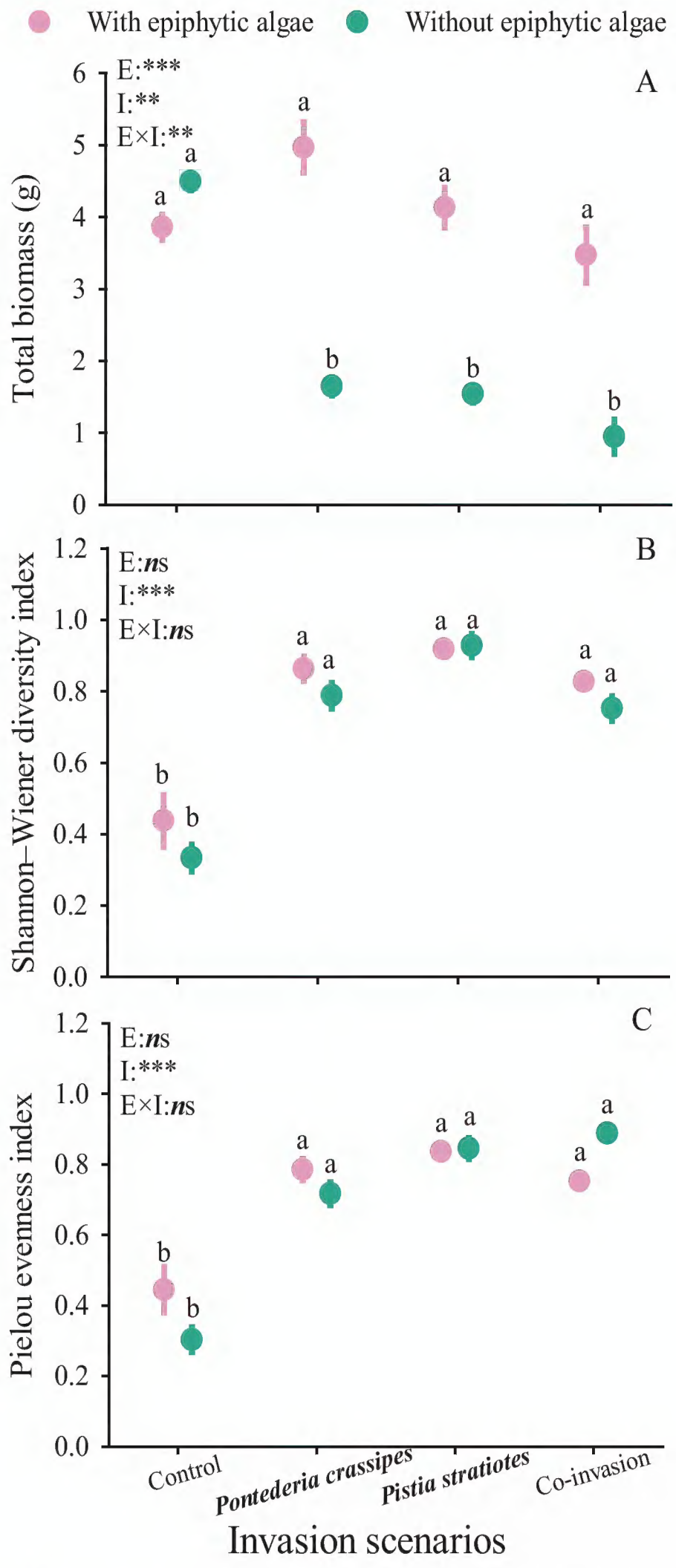

Figure 3. Effects of invasion scenarios (I) and epiphytic algae (E) on indicators of submerged plant communities (mean + SE, n = 5). Control denotes "no invasion"; *Pontederia crassipes* denotes "*Pontederia crassipes* invasion"; *Pistia stratiotes* denotes "*Pistia stratiotes* invasion"; co-invasion denote "co-invasion of *Pontederia crassipes* and *Pistia stratiotes*"; ** denotes "$P < 0.01$"; *** denotes "$P < 0.001$." Different letters indicate significant differences among treatments ($P < 0.05$).

The presence of epiphytic algae caused a negative competitive effect between the submerged plant community and invasion plants under the invasion of *P. crassipes* alone and *P. stratiotes* alone, but positive under the co-invasion (Fig. 4A). On the other hand, the absence of epiphytic algae resulted in a positive competition effect in all invasion scenarios, with co-invasion exerting the highest effect (Fig. 4B).

Characteristics of invasive plants

The findings revealed that epiphytic algae exerted a significant effect on the relative dominance index of invasive plants, but neither invasion scenarios nor epiphytic algae had a significant effect on invasive plant biomass (Table 2). Invasive plants had a higher biomass in the absence of epiphytic algae than in the presence of epiphytic algae (Fig. 5A). The relative dominance index of invasive plants was significantly higher in the absence of epiphytic algae than in the presence of epiphytic algae, with the highest value for co-invasions (Fig. 5B).

Table 2. ANOVA results on the effects of invasion scenarios (I) and epiphytic algae (E) on the indicators of the invasion plants.

Indicators	Invasion scenarios (I)	Epiphytic algae (E)	I × E
Invasion plants biomass	0.623	2.030	0.706
Relative dominance index	2.342	**23.601*****	0.442

†: Significant values of F are shown in bold; *** denotes $P < 0.001$.

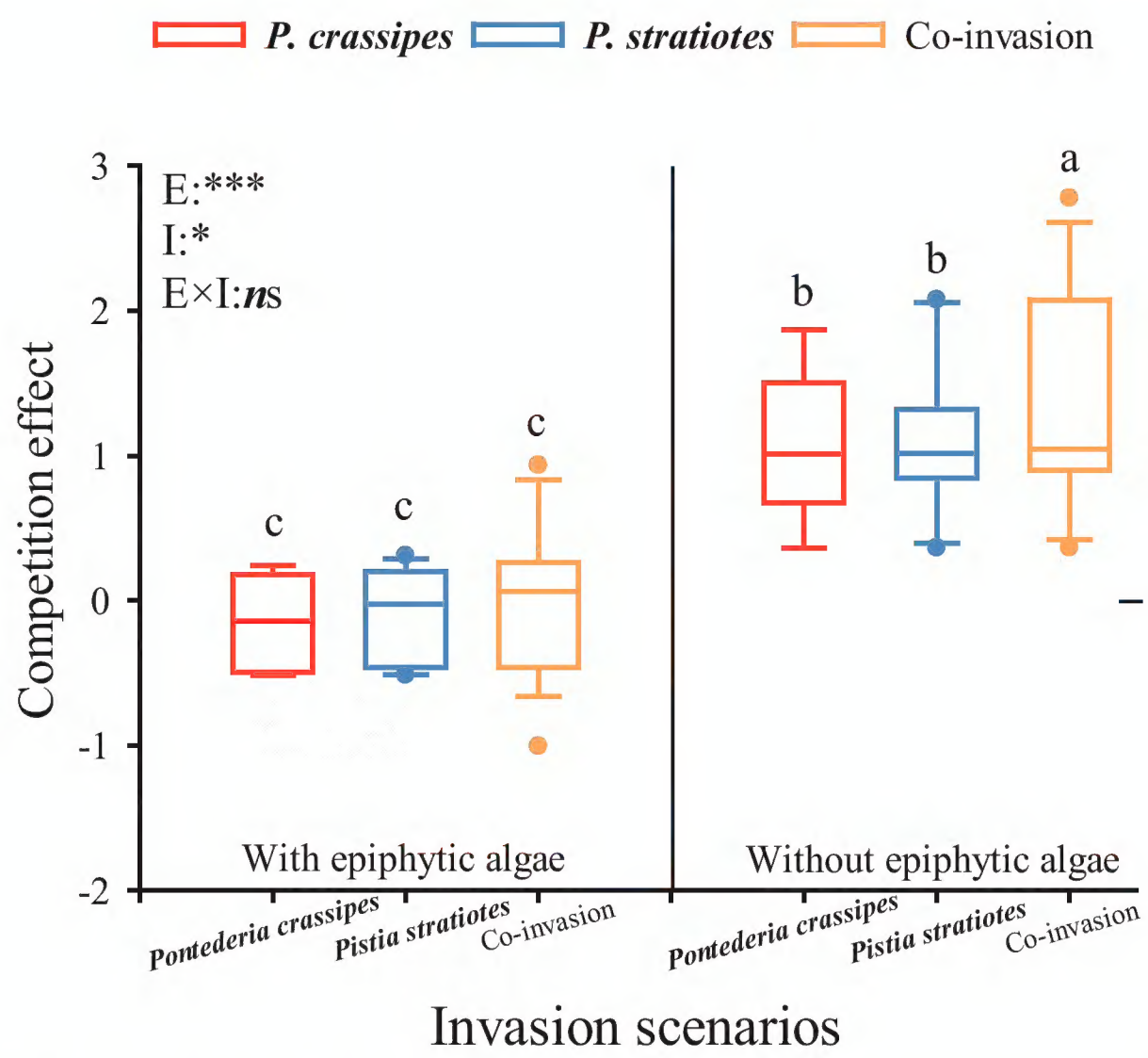

Figure 4. Effects of invasion scenarios (I) and epiphytic algae (E) on competition effect of submerged plant communities (mean + SE, n = 5). *Pontederia crassipes* denotes "*Pontederia crassipes* invasion"; *Pistia stratiotes* denotes "*Pistia stratiotes* invasion"; co-invasion denote "co-invasion of *Pontederia crassipes* and *Pistia stratiotes*"; * denotes "$P < 0.05$"; *** denotes "$P < 0.001$." Different letters indicate significant differences among treatments ($P < 0.05$).

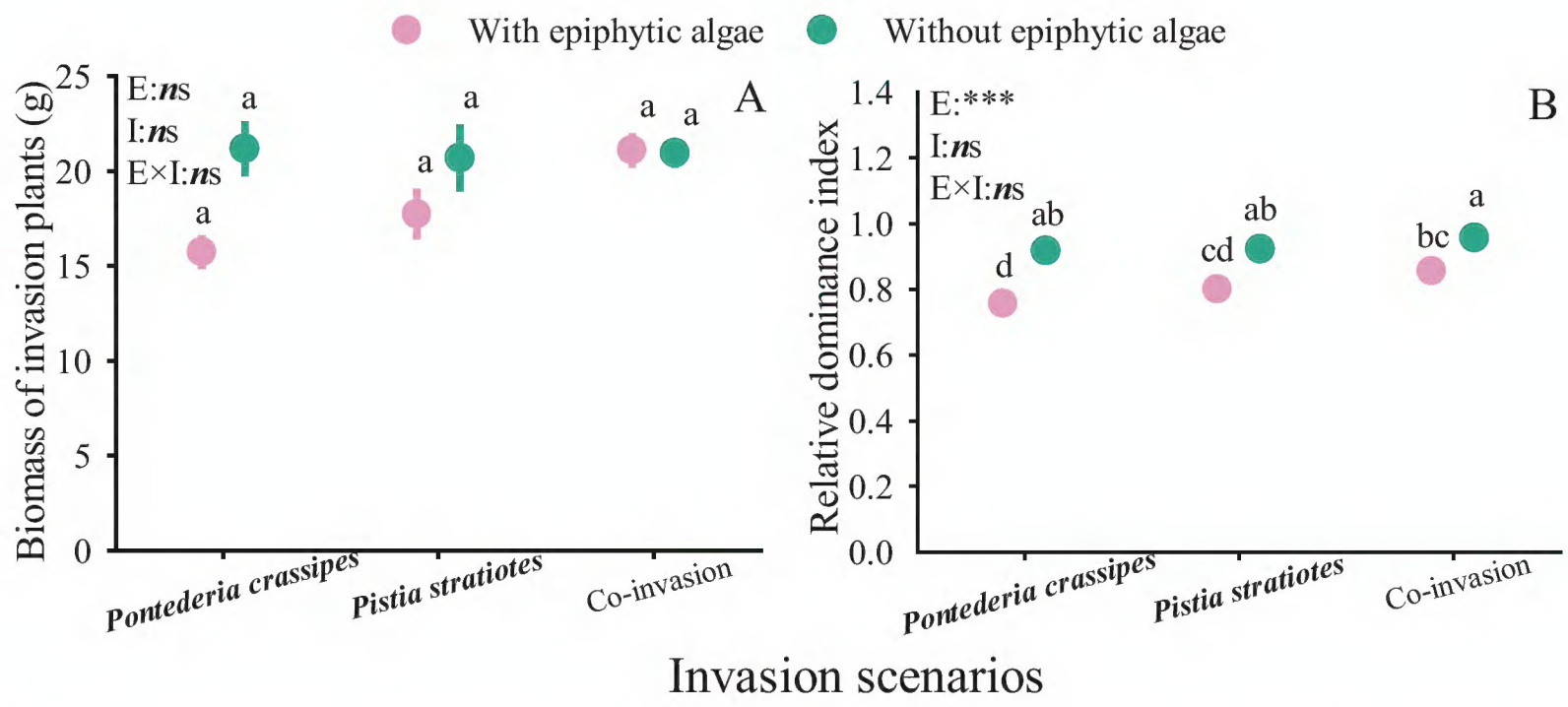

Figure 5. Effects of invasion scenarios (I) and epiphytic algae (E) on biomass and relative dominance index of invasion plants (mean + SE, n = 5). *Pontederia crassipes* denotes "*Pontederia crassipes* invasion"; *Pistia stratiotes* denotes "*Pistia stratiotes* invasion"; co-invasion denotes "co-invasion of *Pontederia crassipes* and *Pistia stratiotes*"; *** denotes "$P < 0.001$." Different letters indicate significant differences among treatments ($P < 0.05$).

Physical and chemical properties of water

Invasive scenarios had significant effects on TN, DO, pH, and transparency, and epiphytic algae exerted significant effects on TP and DO. However, the interaction between the two factors had no significant effect on any of the water quality indicators (Table 3). TN and TP were lowest in the absence of invasion. In the presence of epiphytic algae, TN was highest under the invasion of *P. stratiotes* alone, while in the absence of epiphytic algae, TN was highest under the invasion of *P. crassipes* alone (Fig. 6A). In the presence of epiphytic algae, TP increased with the presence of the invasive plants and was the highest level under co-invasion. Moreover, TP was significantly higher in the presence of epiphytic algae than in the absence of epiphytic algae (Fig. 6B). On the other hand, pH and DO were highest in the absence of invasive plants and significantly decreased in the presence of invasive plants, and transparency was lowest in the presence of *P. stratiotes* alone. The presence or absence of epiphytic algae had no significant effect on pH and transparency (Fig. 6C–E).

Relevance of invasive plants and water quality to submerged plant community

The Pearson correlation analysis revealed that total community biomass was negatively correlated with invasive plant biomass (IB), whereas the community diversity index (SI) and evenness index (PI) were negatively correlated with DO and pH

Table 3 ANOVA results on the effects of invasion scenarios (I) and epiphytic algae (E) on the physical and chemical water properties.

Indicators	Invasion scenarios (I)	Epiphytic algae (E)	I × E
Total nitrogen content	**8.529*****	0.751	1.152
Total phosphorus content	1.220	**4.748***	0.990
Dissolved oxygen	**72.212*****	**6.766***	2.340
pH	**131.515*****	0.945	0.996
Transparency	**19.438*****	0.271	1.754

†: Significant values of F are shown in bold; *** denotes $P < 0.001$, and * denotes $P < 0.05$.

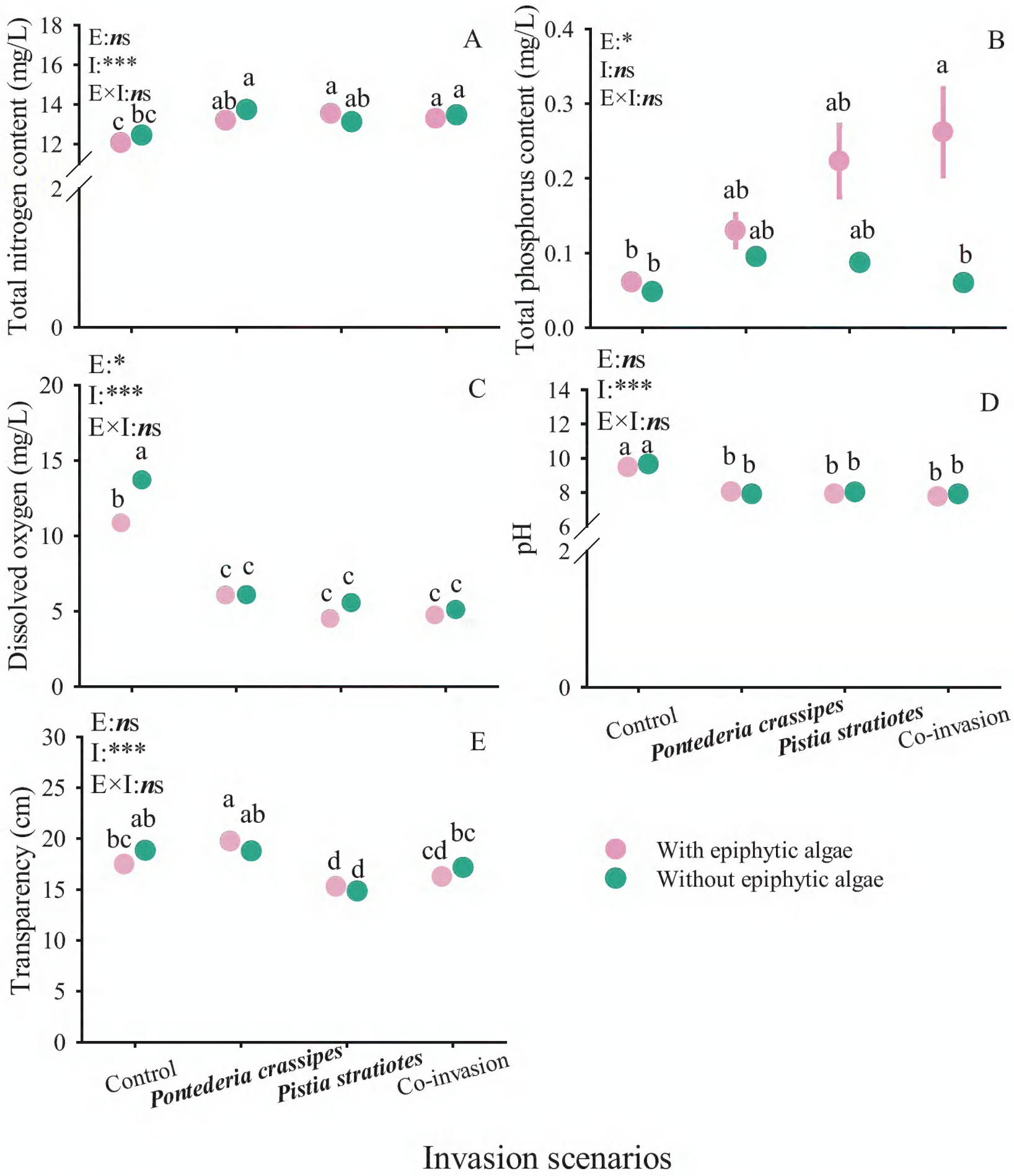

Figure 6. Effects of invasion scenarios (I) and epiphytic algae (E) on Physical and Chemical Properties of Water (mean + SE, n = 5). Control denotes "no invasion"; *Pontederia crassipes* denotes "*Pontederia crassipes* invasion"; *Pistia stratiotes* denotes "*Pistia stratiotes* invasion"; co-invasion denote "co-invasion of *Pontederia crassipes* and *Pistia stratiotes*"; * denotes "$P < 0.05$"; *** denotes "$P < 0.001$." Different letters indicate significant differences among treatments ($P < 0.05$).

but positively correlated with invasive plant biomass (IB). Furthermore, DO and pH were significantly negatively correlated with invasive plant biomass (IB), TN was positively correlated with invasive plant biomass (IB), while transparency and TP had no significant correlation with any other indicators (Fig. 7).

Structural equation models for groups with and without epiphytic algae indicated that TP had a significant positive effect on the submerged plant community in the presence of epiphytic algae ($P < 0.05$, Fig. 8A). In contrast, the submerged plant community was primarily impacted by the significant negative effect of invasive plants and the positive effect of DO in the absence of epiphytic algae ($P < 0.05$, Fig. 8B).

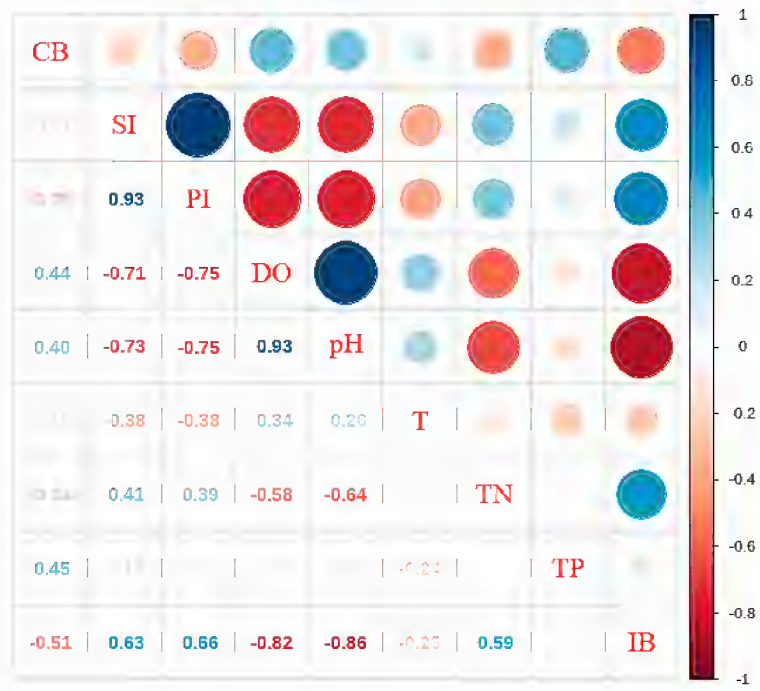

Figure 7. Correlations of the community indicators and physical and chemical water properties with invasive plants. Pairwise correlations of these variables are shown with a color gradient denoting Pearson's correlation coefficients. CB denotes "community total biomass"; SI denotes "Shannon-Wiener diversity index"; PI means "Pielou evenness index"; DO denotes "dissolved oxygen"; T denotes "transparency"; TN denotes "total nitrogen content"; TP means "total phosphorus content"; IB denotes "invasion plant biomass."

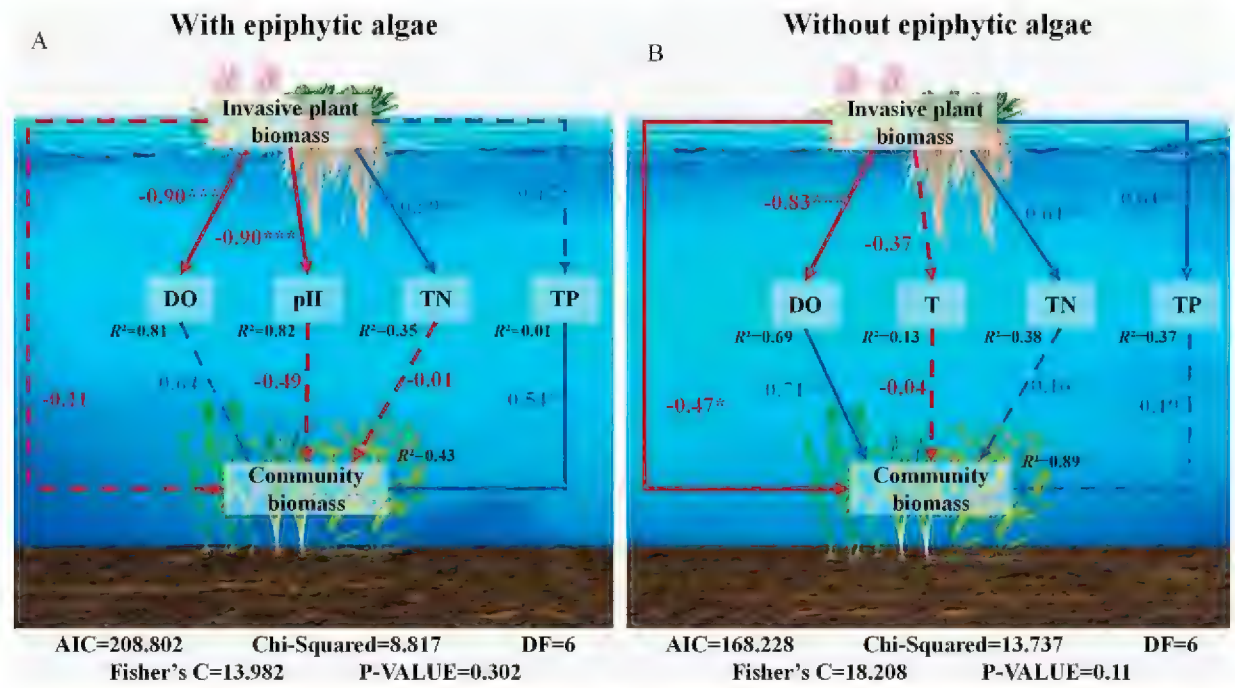

Figure 8. Structural equation modeling diagram of the relationship between the invasive plants, physical and chemical water properties, and community biomass. Rectangles represent measurable variables, and single arrows represent path coefficients; solid lines indicate significant effects ($P < 0.05$), dashed lines indicate non-significant effects, blue lines denote positive effects, red lines denote negative effects, * means $P < 0.05$, ** means $P < 0.01$,*** means $P < 0.001$. DO: dissolved oxygen; TN: total nitrogen content; TP: total phosphorus content; T: transparency.

Discussion

The invasional meltdown hypothesis states that invasive species in multispecies-invaded ecosystems can contribute to each other's detrimental impacts on native communities (Simberloff and Von Holle 1999). Our investigation also discovered that co-invasion had a stronger inhibitory effect on the submerged plant community than a single invasion, so confirming our previous hypothesis. In the absence of invasion, the biomass of the submerged plant community with epiphytic algae was lower than that of the submerged plant community without epiphytic algae. It is hypothesized that epiphytic algae are in a competitive relationship with submerged plant communities in the absence of invasion and, to some extent, limit submerged plant community expansion (Min et al. 2017; Liu et al. 2024). In the presence of epiphytic algae, single-species invasion promoted the growth of the submerged plant community to some extent, and submerged plant biomass was much higher than in the absence

of invasion. The rationale for this finding is that single-species invasion may inhibit the growth of epiphytic algae more than native plants, allowing native plants to compete for more nutrient resources (Lv et al. 2022; Lv et al. 2023).

Numerous studies have demonstrated that the effects of invasions on submerged plant communities can be influenced by other factors, particularly in ecosystems with co-invasion (Petruzzella et al. 2020; Lech and Willig 2021; Huang et al. 2023), which is consistent with the results of our study. We revealed that epiphytic algae promote the growth of submerged plant communities under invasive conditions, implying that epiphytic algae improve the resistance of submerged plant communities to invasion, which concurs with our second hypothesis. This conclusion is supported by the rest of the results (Fig. 3), which demonstrate that except for the co-invasion condition, all native plants mutually reinforce each other in the presence of epiphytic algae. Studies have indicated that submerged plants and epiphytic algae can negatively impact floating plants by limiting nutrients in the water, whereas floating plants can suppress the growth of epiphytic algae through shading and allelopathy, thereby promoting submerged plant growth (Lu et al. 2012; Reynolds and Aldridge 2020; Koleszár et al. 2021). Above a specific threshold, floating plants suppress both epiphytic algae and submerged plants (Koleszár et al. 2021; Szabó et al. 2024), explaining the competitive interaction between submerged plants and biomass reduction under co-invasion by floating plants' condition in this study.

The results demonstrated that plant invasion significantly influences the physical and chemical properties of water, which is consistent with previous research (Lee et al. 2016; Reynolds and Aldridge 2020). Nutrition and light are the two major environmental factors influencing submerged plants (Ersoy et al. 2020; Rao et al. 2020; Wang et al. 2022; Zhao et al. 2022). Transparency affects the intensity of underwater light by altering transmitted light, with invasive floating plants dominating light competition and diminishing underwater light, resulting in reduced transparency (Scheffer et al. 2003; Zhou et al. 2017). Dissolved oxygen is a crucial factor influencing the growth of submerged plants. Floating plants form dense mats on the surface of the water, affecting oxygen exchange with the atmosphere while also influencing the photosynthesis of submerged plants through shading, lowering the DO level (Lu et al. 2012). In addition, pH is intimately linked to the metabolism and reproduction of submerged plants; pH interacts with DO and fluctuates with DO (Xu et al. 2014), consistent with our findings.

Invasive plants possess wider phenotypic plasticity (Szabó et al. 2018; Clark et al. 2023; Carrara et al. 2024), which puts them in a better position to compete with native plants, impacting native plant communities directly. Studies have demonstrated that as native plant richness increases, so does their resistance to invasion (Howeth 2017; Petruzzella et al. 2018). In the present work, we revealed that the native plant community diversity index was positively correlated with invasive plant biomass, because we hypothesized that invasive plants stress the native plant communities, and increasing their richness enhances their resistance to invasion. In future studies, we will further confirm this through experiments. Water quality factors such as DO and pH are intimately tied to the growth of native plants, and invasive plants would indirectly hinder the development of submerged plant communities by altering these factors through shading and emitting allelochemicals (Callaway and Ridenour 2004; Lu et al. 2012), which concur with our findings. In contrast,

TN content was not significantly correlated with the growth of submerged plant communities, potentially because invasive plants acquire their nutrients from the water column, whereas submerged plant communities obtain most of their nutrients from the substrate (Raven 2006; Lu et al. 2012; Zhou et al. 2017). The result of the structural equation modeling showed that epiphytic algae increased the resistance of the submerged plant community to invasion and that the influence of invasive plants on the submerged plant community was negligible in the presence of epiphytic algae.

Conclusion

Plant invasion and epiphytic algae have distinct effects on the development of submerged plant communities. In the absence of plant invasion, epiphytic algae suppressed the growth of submerged plant communities, whereas, in the presence of plant invasion, the total biomass of submerged plant communities with epiphytic algae was significantly higher than that of submerged plant communities without epiphytic algae. Moreover, the total biomass of the communities was the lowest under co-invasion conditions. This finding demonstrates that co-invasion exacerbates the inhibition of the growth of submerged plant communities, while epiphytic algae lessen this inhibition. The current findings on the effects of epiphytic algae on submerged plant communities against invasion provide a scientific basis for native plant restoration.

Acknowledgments

We thank all those who provided help and support for this study.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was supported by the Fundamental Research Funds for the Central Universities (QNTD202510), the Fundamental Research Funds for the Central Universities (QNTD202304), the National Key Research and Development Program of China (2021YFC2600400), the China Major Science and Technology Program for Water Pollution Control and Treatment (2017ZX07602-004-003).

Author contributions

Yi-Luan Shen: Writing - original draft, Investigation. Jing-Fang Cai: Visualization, Methodology. Jing-Jing Xue: Visualization, Methodology. Xiao-Li Yang: Methodology. Da-Zhi Wang: Methodology. Hong-Li Li: Writing - review and editing, Resources, Project administration.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Alena SG, Sven T, Marta MAN, Sabine H (2025) Epiphyton phenology determines the persistence of submerged macrophytes: Exemplified in temperate shallow lakes. Limnology and Oceanography 70(3): 764–774. https://doi.org/10.1002/lno.12808

Asaeda T, Sultana M, Manatunge J, Fujino T (2004) The effect of epiphytic algae on the growth and production of *Potamogeton perfoliatus* L. in two light conditions. Environmental and Experimental Botany 52(3): 225–238. https://doi.org/10.1016/j.envexpbot.2004.02.001

Callaway RM, Ridenour WM (2004) Novel weapons: Invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8): 436–443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Carrara L, Moi DA, Figueiredo BRS, van Kleunen M, Pastorini LH, Romagnolo MB, Souza LA (2024) Tolerance to drought and flooding events provides a competitive advantage for an invasive over a native plant species. Freshwater Biology 69(3): 425–434. https://doi.org/10.1111/fwb.14221

Cattaneo A, Galanti G, Gentinetta S, Susana A (1998) Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. Freshwater Biology 39(4): 725–740. https://doi.org/10.1046/j.1365-2427.1998.00325.x

Clark CD, Moles AT, Fazlioglu F, Brandenburger CR, Hartley S (2023) Rapid loss of phenotypic plasticity in the introduced range of the beach daisy, *Arctotheca populifolia.* Journal of Ecology 112(1): 28–40. https://doi.org/10.1111/1365-2745.14210

Dai YH, Yang SB, Zhao D, Hu CM, Xu W, Anderson DM, Li Y, Song XP, Boyce DG, Gibson L, Zheng CM, Feng L (2023) Coastal phytoplankton blooms expand and intensify in the 21st century. Nature 615(7951): 280–284. https://doi.org/10.1038/s41586-023-05760-y

Ersoy Z, Scharfenberger U, Baho DL, Bucak T, Feldmann T, Hejzlar J, Levi EE, Mahdy A, Nõges T, Papastergiadou E, Stefanidis K, Šorf M, Søndergaard M, Trigal C, Jeppesen E, Beklioğlu M (2020) Impact of nutrients and water level changes on submerged macrophytes along a temperature gradient: A Pan-European mesocosm experiment. Global Change Biology 26(12): 6831–6851. https://doi.org/10.1111/gcb.15338

Fleming JP, Dibble ED (2014) Ecological mechanisms of invasion success in aquatic macrophytes. Hydrobiologia 746(1): 23–37. https://doi.org/10.1007/s10750-014-2026-y

Fletcher J, Willby N, Oliver D, Quilliam RS (2023) Engineering aquatic plant community composition on floating treatment wetlands can increase ecosystem multifunctionality. Environmental Research 243: 117818. https://doi.org/10.1016/j.envres.2023.117818

Howeth JG (2017) Native species dispersal reduces community invasibility by increasing species richness and biotic resistance. Journal of Animal Ecology 86(6): 1380–1393. https://doi.org/10.1111/1365-2656.12733

Huang XL, Ke F, Lu J, Xie HM, Zhao Y, Yin CY, Guan BH, Li KY, Jeppesen E (2023) Underwater light attenuation inhibits native submerged plants and facilitates the invasive co-occurring plant *Cabomba caroliniana.* Diversity & Distributions 29(4): 543–555. https://doi.org/10.1111/ddi.13678

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L (1997) Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 32: 151–164. https://doi.org/10.1023/A:1017046130329

Koleszár G, Borics G, Várbíró G, Nagy Z, Peeters ETHM, Birk S, Szabó S (2021) The Role of Epiphytic Algae and Grazing Snails in Stable States of Submerged and of Free-Floating Plants. Ecosystems 25(6): 1371–1383. https://doi.org/10.1007/s10021-021-00721-w

Kuehne LM, Olden JD, Rubenson ES (2016) Multi-trophic impacts of an invasive aquatic plant. Freshwater Biology 61(11): 1846–1861. https://doi.org/10.1111/fwb.12820

Lech JD, Willig MR (2021) Unravelling the effects of multiple types of disturbance on an aquatic plant metacommunity in freshwater lakes. Freshwater Biology 66(7): 1395–1409. https://doi.org/10.1111/fwb.13725

Lee MR, Bernhardt ES, Bodegom PM, Cornelissen JHC, Kattge J, Laughlin DC, Niinemets Ü, Peñuelas J, Reich PB, Yguel B, Wright JP (2016) Invasive species' leaf traits and dissimilarity from natives shape their impact on nitrogen cycling: A meta-analysis. The New Phytologist 213(1): 128–139. https://doi.org/10.1111/nph.14115

Li BH, Xu DD, Zhou XH, Yin YJ, Feng L, Liu YZ, Zhang LQ (2023) Environmental behaviors of emerging contaminants in freshwater ecosystem dominated by submerged plants: A review. Environmental Research 227: 115709. https://doi.org/10.1016/j.envres.2023.115709

Li C, Li Y, Xu ZL, Zhong SS, Cheng HY, Liu J, Yu YL, Wang CY, Du DL (2024) The effects of co-invasion by three Asteraceae invasive alien species on plant taxonomic and functional diversity in herbaceous ruderal communities in southern Jiangsu, China. Biologica Futura. https://doi.org/10.1007/s42977-024-00202-w

Liao LB, Yu DS, Xu L, Hu Q, Liang TJ, Chen LD, Zhu QP, Liu SP, Zhong AW (2024) Submersed macrophytes *Vallisneria natans* and *Vallisneria spinulosa* improve water quality and affect microbial communities in sediment and water columns. Heliyon 10(3): e25942. https://doi.org/10.1016/j.heliyon.2024.e25942

Liu H (2021) Physiological and ecological mechanisms of submerged plants adapting to low light environments in eutrophic lakes. PhD Thesis. University of Chinese Academy of Sciences.

Liu XY, Sun T, Yang W, Li XX, Ding JW, Fu XT (2024) Meta-analysis to identify inhibition mechanisms for the effects of submerged plants on algae. Journal of Environmental Management 355: 120480. https://doi.org/10.1016/j.jenvman.2024.120480

Lu J, Wang ZX, Xing W, Liu GH (2012) Effects of substrate and shading on the growth of two submerged macrophytes. Hydrobiologia 700(1): 157–167. https://doi.org/10.1007/s10750-012-1227-5

Lv T, Fan SF, Wang HY, Li DX, Wang QY, Lei XY, Liu CH, Yu D (2022) Invasion of water hyacinth and water lettuce inhibits the abundance of epiphytic algae. Diversity & Distributions 28(8): 1650–1662. https://doi.org/10.1111/ddi.13527

Lv T, Wang HY, Wang QY, Li DX, Gao CY, Zhang TT, Lei XY, Liu CH (2023) Invasive submerged plant has a stronger inhibitory effect on epiphytic algae than native plant. Biological Invasions 26(4): 1001–1014. https://doi.org/10.1007/s10530-023-03225-x

Ma XW, Liu HM, Wang LG, Liu CH (2023) Effects of clonal integration on characteristics of free-floating and submerged plant communities under different nutrient conditions. Flora 298: 152205. https://doi.org/10.1016/j.flora.2022.152205

Min FL, Zuo JC, Zhang Y, Lin QW, Liu BY, Sun J, Zeng L, He F, Wu ZB (2017) The Biomass and Physiological Responses of *Vallisneria natans* (Lour.) Hara to Epiphytic Algae and Different Nitrate-N Concentrations in the Water Column. Water 9(11): 863. https://doi.org/10.3390/w9110863

Peng QT, Huo BB, Yang H, Xu ZY, Mao HZ, Yang SW, Dai YT, Li ZQ, Deng XW (2023) Increased invasion of submerged macrophytes makes native species more susceptible to eutrophication in freshwater ecosystems. The Science of the Total Environment 909: 168658. https://doi.org/10.1016/j.scitotenv.2023.168658

Petruzzella A, Rodrigues TASSR, Leeuwen CHA, Esteves FA, Figueiredo-Barros MP, Bakker ES (2020) Species identity and diversity effects on invasion resistance of tropical freshwater plant communities. Scientific Reports 10: 5626. https://doi.org/10.1038/s41598-020-62660-1

Petruzzella A, Manschot J, van Leeuwen CHA, Grutters BMC, Bakker ES (2018) Mechanisms of Invasion Resistance of Aquatic Plant Communities. Frontiers in Plant Science 9: 134. https://doi.org/10.3389/fpls.2018.00134

Phillips G, Willby N, Moss B (2016) Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? Aquatic Botany 135: 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004

Qian ZH, Li Y, Yang JS, Shi T, Li ZZ, Chen JM (2022) The chromosome-level genome of a free-floating aquatic weed *Pistia stratiotes* provides insights into its rapid invasion. Molecular Ecology Resources 22(7): 2732–2743. https://doi.org/10.1111/1755-0998.13653

Rao QY, Su HJ, Deng XW, Xia WL, Wang LT, Cui WJ, Ruan LW, Chen J, Xie P (2020) Carbon, Nitrogen, and Phosphorus Allocation Strategy Among Organs in Submerged Macrophytes Is Altered by Eutrophication. Frontiers in Plant Science 11: 524450. https://doi.org/10.3389/fpls.2020.524450

Raven JA (2006) Nutritional strategies of submerged benthic plants: The acquisition of C, N and P by rhizophytes and haptophytes. The New Phytologist 88(1): 1–30. https://doi.org/10.1111/j.1469-8137.1981.tb04564.x

Reynolds SA, Aldridge DC (2020) Embracing the Allelopathic Potential of Invasive Aquatic Plants to Manipulate Freshwater Ecosystems. Frontiers in Environmental Science 8: 551803. https://doi.org/10.3389/fenvs.2020.551803

Scheffer M, Szabó S, Gragnani A, Nes EHv, Rinaldi S, Kautsky N, Norberg J, Roijackers RMM, Franken RJM (2003) Floating plant dominance as a stable state. Proceedings of the National Academy of Sciences of the United States of America 100: 4040-4045. https://doi.org/10.1073/pnas.0737918100

Shen YL, Zhang SY, Yuan XF, Sun K, Cai JF, Xue JJ, Zhang Y, A S-H, Yang L-J, Cheng R, Li H-L, Lei G-C (2023) Flat-leaf submerged plants are more sensitive to invasion intensity and water nutrition levels than needle-leaf ones. Hydrobiologia 850(18): 3849–3863. https://doi.org/10.1007/s10750-023-05226-2

Simberloff D, Von Holle B (1999) Positive Interactions of Nonindigenous Species: Invasional Meltdown? Biological Invasions 1(1): 21–32. https://doi.org/10.1023/A:1010086329619

Song YZ, Wang JQ, Gao YX (2017) Effects of epiphytic algae on biomass and physiology of *Myriophyllum spicatum* L. with the increase of nitrogen and phosphorus availability in the water body. Environmental Science and Pollution Research International 24(10): 9548–9555. https://doi.org/10.1007/s11356-017-8604-6

Szabó S, Peeters ETHM, Várbíró G, Borics G, Lukács BA (2018) Phenotypic plasticity as a clue for invasion success of the submerged aquatic plant *Elodea nuttallii.* Plant Biology 21(1): 54–63. https://doi.org/10.1111/plb.12918

Szabó S, Csizmár A, Koleszár G, Oláh V, Birk S, Peeters ETHM (2024, June) Density-dependent facilitation and inhibition between submerged and free-floating plants. Hydrobiologia 851(11): 2749–2760. https://doi.org/10.1007/s10750-024-05491-9

Wang D (2016) Studies on interspecific competition and synergism during invasion by *Chromolaena odorata* (L.). MSc Thesis. South China Agricultural University.

Wang CY, Wei M, Wang S, Wu BD, Cheng HY (2020) *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L. antagonistically affect community stability and community invasibility under the co-invasion condition. The Science of the Total Environment 716: 137128. https://doi.org/10.1016/j.scitotenv.2020.137128

Wang LT, Rao QY, Su HJ, Ruan LW, Deng XW, Liu JR, Chen J, Xie P (2022) Linking the network topology of plant traits with community structure, functioning, and adaptive strategies of submerged macrophytes. The Science of the Total Environment 850: 158092. https://doi.org/10.1016/j.scitotenv.2022.158092

Wang CY, Li Y, Li C, Zhong SS, Xu ZL, Yu YL, Du DL (2023) A method for quantifying relative competitive advantage and the combined effect of co-invasion for two invasive plants. Plant Diversity 45(3): 3. https://doi.org/10.1016/j.pld.2023.01.005

Wei M, Wang S, Xiao HG, Wu BD, Jiang K, Wang CY (2020) Co-invasion of daisy fleabane and Canada goldenrod pose synergistic impacts on soil bacterial richness. Journal of Central South University 27(6): 1790–1801. https://doi.org/10.1007/s11771-020-4408-9

Xu JP, Zhang XP, Zeng B, Yuan SH, Liu JH, Liu MZ (2014) Effects of light and dissolved oxygen on the phenotypic plasticity of *Alternanthera philoxeroides* in submergence conditions. Acta Ecologica Sinica 34(2): 258–268. https://doi.org/10.5846/stxb201301110081

Yan YM, Oduor AMO, Li F, Xie YH, Liu YJ (2022) Opposite effects of nutrient enrichment and an invasive snail on the growth of invasive and native macrophytes. Ecological Applications 34(1): e2737. https://doi.org/10.1002/eap.2737

Yuan YF, Guo WH, Ding WJ, Du N, Luo YJ, Liu J, Xu F, Wang RQ (2013) Competitive interaction between the exotic plant *Rhus typhina* L. and the native tree *Quercus acutissima* Carr. in Northern China under different soil N:P ratios. Plant and Soil 372(1-2): 389–400. https://doi.org/10.1007/s11104-013-1748-3

Yuan GX, Sun LJ, Guo PQ, Xiao JJ, Meng WS, Ren B, Wu AP, Li YZ, Fu H, Jeppesen E (2023) How Eutrophication Promotes Exotic Aquatic Plant Invasion in the Lake Littoral Zone? Environmental Science & Technology 57(21): 8002–8014. https://doi.org/10.1021/acs.est.2c09486

Zhang JW, Liu KX, Li YG, Deng H, Huang DY, Zhang JB (2023) Characterization and seasonal variation in biofilms attached to leaves of submerged plant. World Journal of Microbiology & Biotechnology 40(1): 19. https://doi.org/10.1007/s11274-023-03832-9

Zhao JS, Yang P, Lin YY, Zhu XY, Wang JX, Gan XY, Zheng XY, Zhao M, Fan CZ, Du LN, Miu HY (2022) The effect of underwater supplemental light on the growth of *V. spinulosa* Yan and the restoration process of water. Process Safety and Environmental Protection 169: 328–336. https://doi.org/10.1016/j.psep.2022.11.043

Zhong SS, Xu ZL, Yu YL, Cheng HY, Wei M, Wang S, Du DL, Wang CY (2022) Acid deposition at higher acidity weakens the antagonistic responses during the co-decomposition of two Asteraceae invasive plants. Ecotoxicology and Environmental Safety 243: 114012. https://doi.org/10.1016/j.ecoenv.2022.114012

Zhou J, Pan X, Xu HT, Wang Q, Cui LJ (2017) Invasive *Eichhornia crassipes* Affects the Capacity of Submerged Macrophytes to Utilize Nutrients. Sustainability 9(4): 565. https://doi.org/10.3390/su9040565